GEOGRAPHIC SPATIAL AUTOCORRELATION OF MORPHOLOGICAL CHARACTERS IN *HEMEROCALLIS HAKUUNENSIS* (LILIACEAE)

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ABSTRACT

Spatial autocorrelation analysis of 12 quantitative characters among 30 populations of *Hemerocallis hakuunensis* was conducted to understand better their geographic variation patterns. There are two types of relationships between the mean values of the characters measured and their spatial autocorrelations: (1) significant heterogeneity of means with significant autocorrelation (mostly floral characters); and (2) significant heterogeneity of means with no significant autocorrelation (mostly vegetative characters). Perianth size shows significant north-south clinal variation and width of inner and outer perianth show a typical monotonic decline from significant positive autocorrelation at interpopulation distance of 67 to 107 km to significant negative autocorrelation at distances of 221 to 357 km. The results might result from the combinations of gene flow, genetic drift, and/or selective forces operated in populations of *H. hakuunensis*.

RESUMEN

Se realizó un análisis de correlación espacial de 12 caracteres cuantitativos en 30 poblaciones de *Hemerocallis hakuunensis* para comprender mejor sus patrones de variación geográfica. Hay dos tipos de relaciones entre los valores medios de los caracteres medidos y sus autocorrelaciones espaciales: (1) heterogeneidad significativa de las medias con autocorrelación significativa (la mayoría en caracteres florales); y (2) heterogeneidad significativa de las medias sin autocorrelación significativa (la mayoría en caracteres vegetativos). El tamaño del perianto muestra una variación clinal norte-sur significativa y la anchura del perianto interno y externo muestra una disminución monotónica típica desde una autocorrelación positiva significativa en distancias interpoblacionales de 67 a 107 km hasta una autocorrelación negativa significativa en distancias de 221 a 357 km. Los resultados podrían derivarse de las combinaciones de flujo genético, deriva genética y/o fuerzas selectivas que operan en las poblaciones de *H. hakuunensis*.

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INTRODUCTION

In Korea, five species of *Hemerocallis* are recognized on the basis of morphological analysis (12 quantitative and seven qualitative characters), fieldwork, and examination of Japanese herbarium specimens (Chung & Kang 1994; Kang & Chung 1997a). These are *H. hakuunensis* Nakai, *H. thunbergii* Baker, *H. middendorffii* Tr. et Mey., *H. hongdoensis* M. Chung & S. Kang, and *H. taeanensis* S. Kang & M. Chung.

Hemerocallis hakuunensis is Korean endemic species that commonly grows at the margins of pine-oak forests, grasslands, and disturbed habitats such as chest-nut orchards in southern, central, and northwestern Korea (Chung & Kang 1994). Among the four Korean *Hemerocallis* species, populations of *H. hakuunensis* are the most variable in their inflorescence and floral morphology (Kang & Chung 1994). In addition, Chung and Kang (1994) noted that populations of *H. hakuunensis* with larger flowers are generally located in the central Korean Peninsula, while populations with smaller flowers occur in southern Korea. These patterns of geographic variation in morphological characters of the species require further study for a better understanding the species. A detailed study of the patterns of geographic variation of quantitative morphology in *H. hakuunensis* is reported here.

The principal method of analysis for this purpose is spatial autocorrelation analysis. Spatial autocorrelation statistics are summary measures of the dependence of the value of a particular variable at one location on the value of that same variable at other nearby locations. The most commonly used measure is Moran's (1950) autocorrelation coefficient *I*, in which geographic neighbors are compared in terms of their deviation from the mean of all observations. The method has been applied in a variety of fields including biogeography, political science, ecology, archaeology, and econometrics (Cliff & Ord 1981; Griffith 1988). Recently, this method of character analysis has been employed in the analysis of morphological characters and the spatial dispersal patterns of genetic variations because it can provide a detailed picture of geographic variation in characters (Sokal & Oden 1978a,b; Sokal et al. 1986; Jensen 1986; Chung 1995, 1996). Sokal and Oden (1978a) described five correlogram patterns of geographic variation of characters. Cline is a gradual change from the highest positive *I* to the lowest negative *I*, across all distance groups. Depression is nothing but a circular cline, with the lowest negative *I* between the shortest and longest distances, not the longest distance. Double depression is on the whole quite similar to that of the depression, with low *I* in a certain distance from which another low *I* was separated. Intrusion pattern shows positive *I*s at a certain distance, because of the homogeneity within the distance, with a sharply decreasing *I* bordering the distance. Crazy quilt pattern shows high *I*s surrounded by low *I*s, *vice versa*, which yields no significant *I*s at all.

The purpose of this study is to determine whether or not the 12 quantitative characters recorded for *H. hakuunensis* by Chung and Kang (1994) and Kang and Chung (1994) show any geographic patterns such as clines, depression, double depression, intrusions, and crazy quilt patterns (Sokal & Oden 1978a).

MATERIALS AND METHODS

Thirty populations representing the geographic range of *H. hakuunensis* were used for this study (Fig. 1). Measurements of 12 quantitative characters (Table 1; also see Table 2 in Chung & Kang 1994) were taken on each of 10 randomly selected individuals directly from their natural habitats from 1991 to 1995. Voucher specimens of all collections are deposited at the herbarium of Gyeongsang National University (GNUC).

For spatial autocorrelation analysis, mean values were assigned to each population for the 12 characters. Every possible pair of populations was considered as a join or a connection and was assigned to one of six distance classes based on the geographic distance between them. These six distance classes were constructed by equalizing sample sizes among the classes. The distance classes are $0<76$, $76<102$, $102<136$, $136<169$, $169<221$, and $221<357$ km. Moran's *I* values were calculated for interpopulational distance classes by

$$I = N \sum_{i}\sum_{j} (W_{ij} \Sigma_i Z_j) (\sum_{i}\sum_{j} W_{ij} \Sigma Z_i^2)^{-1}$$

(Sokal & Oden 1978a). *N* is the number of populations, W_{ij} is the join on weighting matrix, where W_{ij} is set as one if *i*th and *j*th population are in the distance class and zero otherwise, $Z_i = X_i - \overline{X}$, $Z_j = X_j - \overline{X}$, the variables X_i and X_j are the mean scores for *i*th and *j*th population, respectively, and X is the mean score for all populations. The value of *I* ranges between +1 (complete positive autocorrelation, i.e., paired populations have identical values for all characters) and -1 (complete negative autocorrelation). Each *I* value was used to test significant deviations from the expected values, $E(I)=-1/(N-1)$ (Cliff & Ord 1981). The neighboring populations in the distance class considered, with a significant positive value of Moran's *I* have similar scores, whereas those with a significant negative value should have different scores. Overall significance of individual correlograms was tested using Bonferroni's criteria (Sakai & Oden 1983). All calculations and statistical analyses were performed using the SAAP program (ver. 4.3) written by D. Wartenberg.

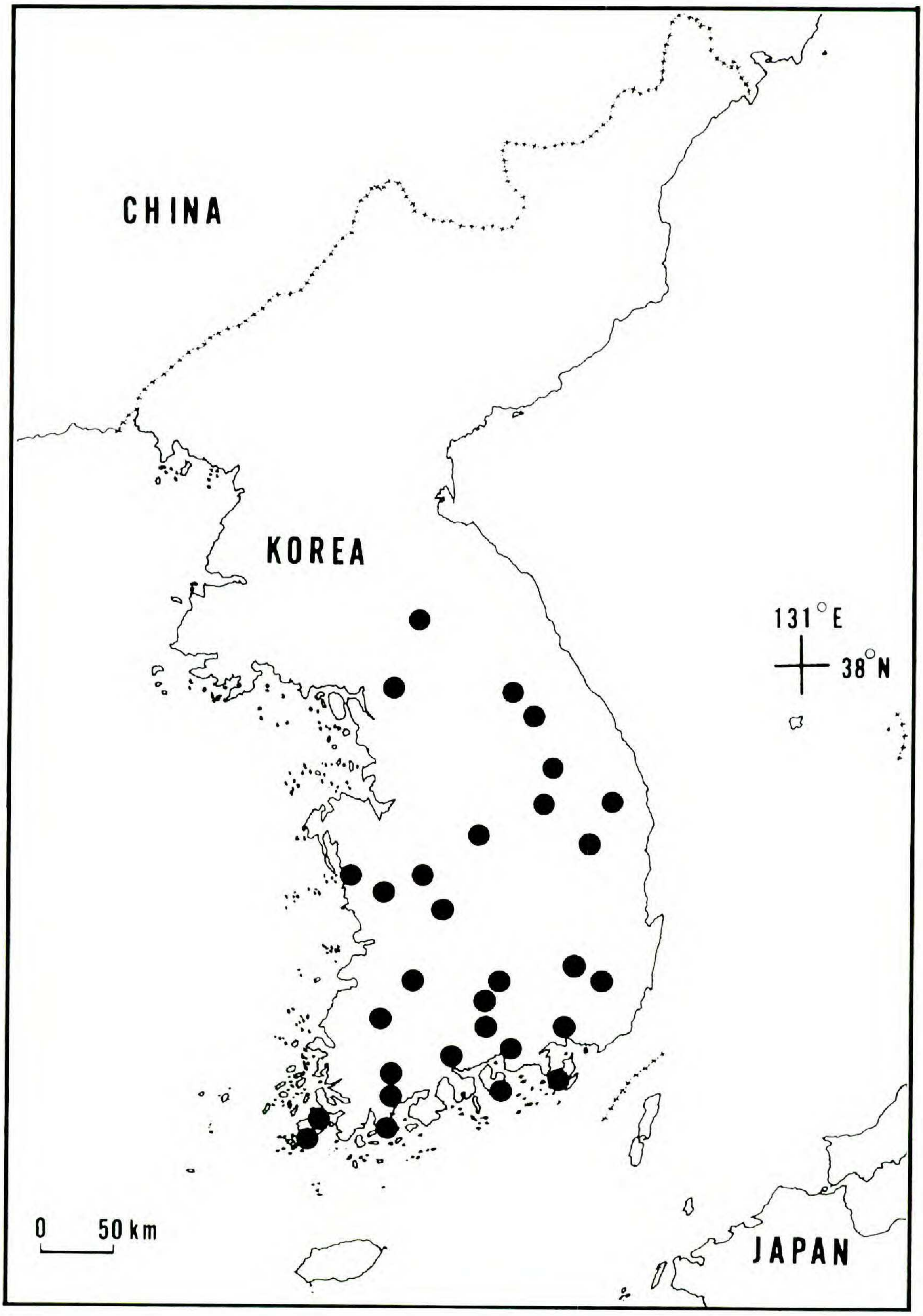

FIG. 1. The location of 30 examined populations of *Hemerocallis hakuunensis*.

TABLE 1. List of 12 quantitative characters used in the spatial autocorrelation analysis.

Acronym	Character derivation	Unit or category
PSH	Plant (scape) height	m
LIF	Length of inflorescence minus flowers	cm
NBS	Number of bracts/scape	#
NFS	Number of flowers/scape	#
LLB	Length of the lowest bracts	cm
WLB	Width of the lowest bracts	cm
LPO	Length of the perianth tube enclosing an ovary	cm
LIP	Length of the inner perianth	cm
WIP	Width of the inner perianth	cm
LOP	Length of the outer perianth	cm
WOP	Width of the outer perianth	cm
WWL	Width of the widest leaves	cm

RESULTS

Correlograms for each character are presented in Figures 2–3. Moran's I was significant in 26 of 72 cases (36%). The overall correlogram for width of the lowest bracts (WLB), length of the inner perianth (LIP), width of inner perianth (WIP), length of outer perianth (LOP), width of the outer perianth (WOP), and width of the widest leaves (WWL) was significant ($P < 0.01$). As presented in Figures 2–3, plant (scape) height (PSH), length of inflorescence minus flowers (LIF), and length of the perianth tube enclosing an ovary (LPO) show depression correlograms (Sokal & Oden 1978b). On the other hand, number of bracts per scape (NBS), number of flower per scape (NFS), WIP, and WOP represent clinal variation with two, WIP and WOP, significantly autocorrelated (Figs. 2–3). In addition, it is apparent that each floral size character shows a similar pattern of geographic variation. For example, LIP and LOP, WLP and WOP (Fig. 3) revealed significant positive autocorrelation (localities connected for that distance class had similar values) for distance classes 1 to 3, followed by a steady decline until significant negative autocorrelation (localities for that distance class have dissimilar values) are recorded for distance class 5. Although LIP and LOP show increase in autocorrelation between distance classes 5 and 6, significant negative autocorrelations are also observed on these distance classes (Fig. 3). As seen in Figures 2–3, length of the lowest bract (LLB) has a crazy quilt correlogram pattern with no significant autocorrelations, whereas width of the lowest bracts (WLB) and WWL display intrusion patterns.

DISCUSSION

There were two types of relationships between means and spatial autocorrelations observed. The first pattern of significant heterogeneity of means with significant autocorrelation was observed for WLB, LIP, WIP,

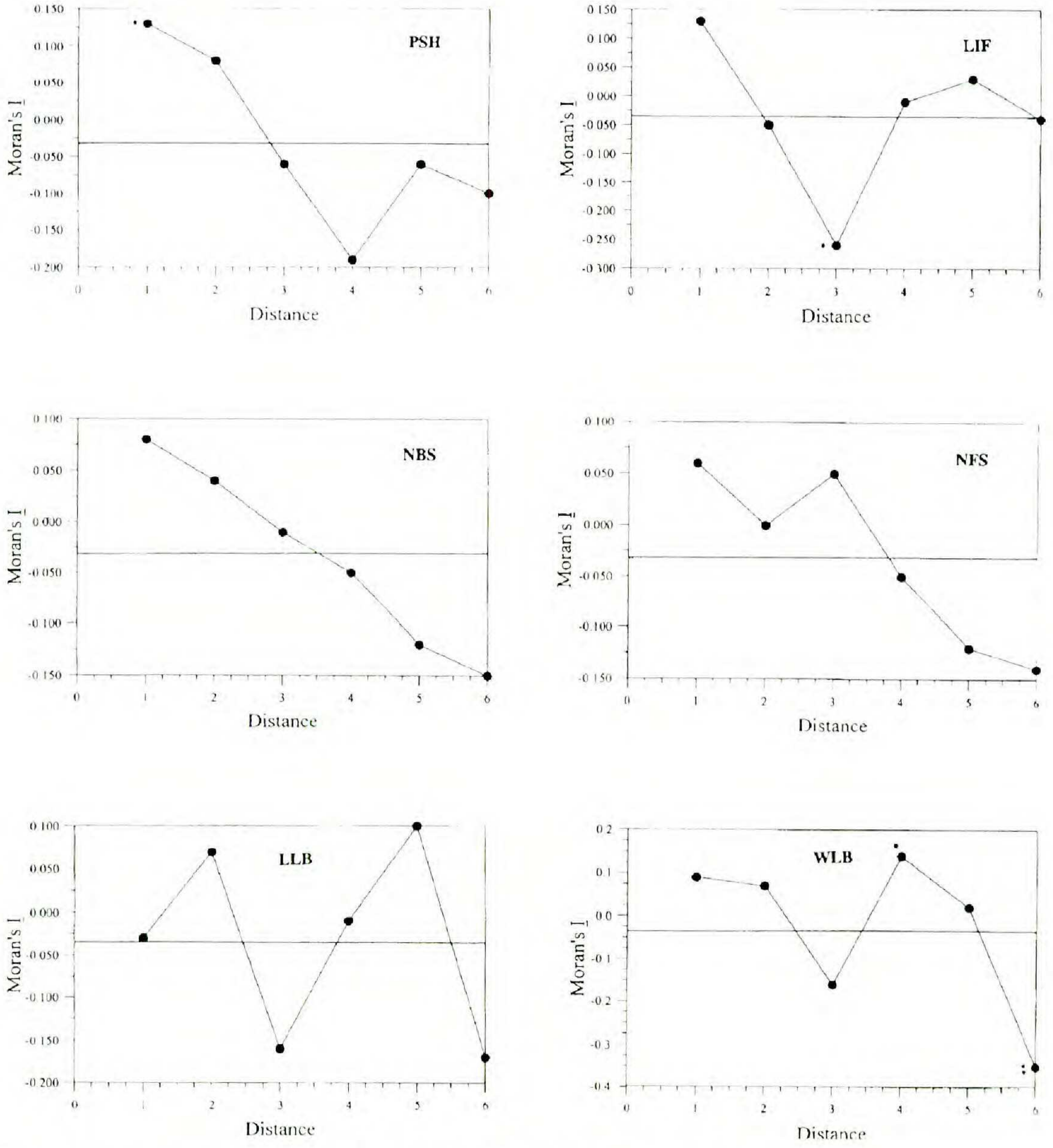

FIG. 2. Correlograms for PSH, LIF, NBS, NFS, LLB, and WLB. Significant autocorrelation coefficients ($P < 0.05$) are indicated by asterisks.

LOP, WOP, and WWL. The second pattern of significant heterogeniety of means with no significant autocorrelation is found for the other six characters. Sokal and Oden (1978b) suggested biological explanations for each of the two types of patterns. The first could result from migration, founder effects, and selective agents. The second type of relationship between means and autocorrelations could result from drift, weak migration and selection, frequent local extinctions followed by the establishment of new patches by founders, or from selection in isolated, patchy environments. Except for LLB, all characters show short distance positive autocorrelations, indicating that migration could be operating over the distances. Certainly in some

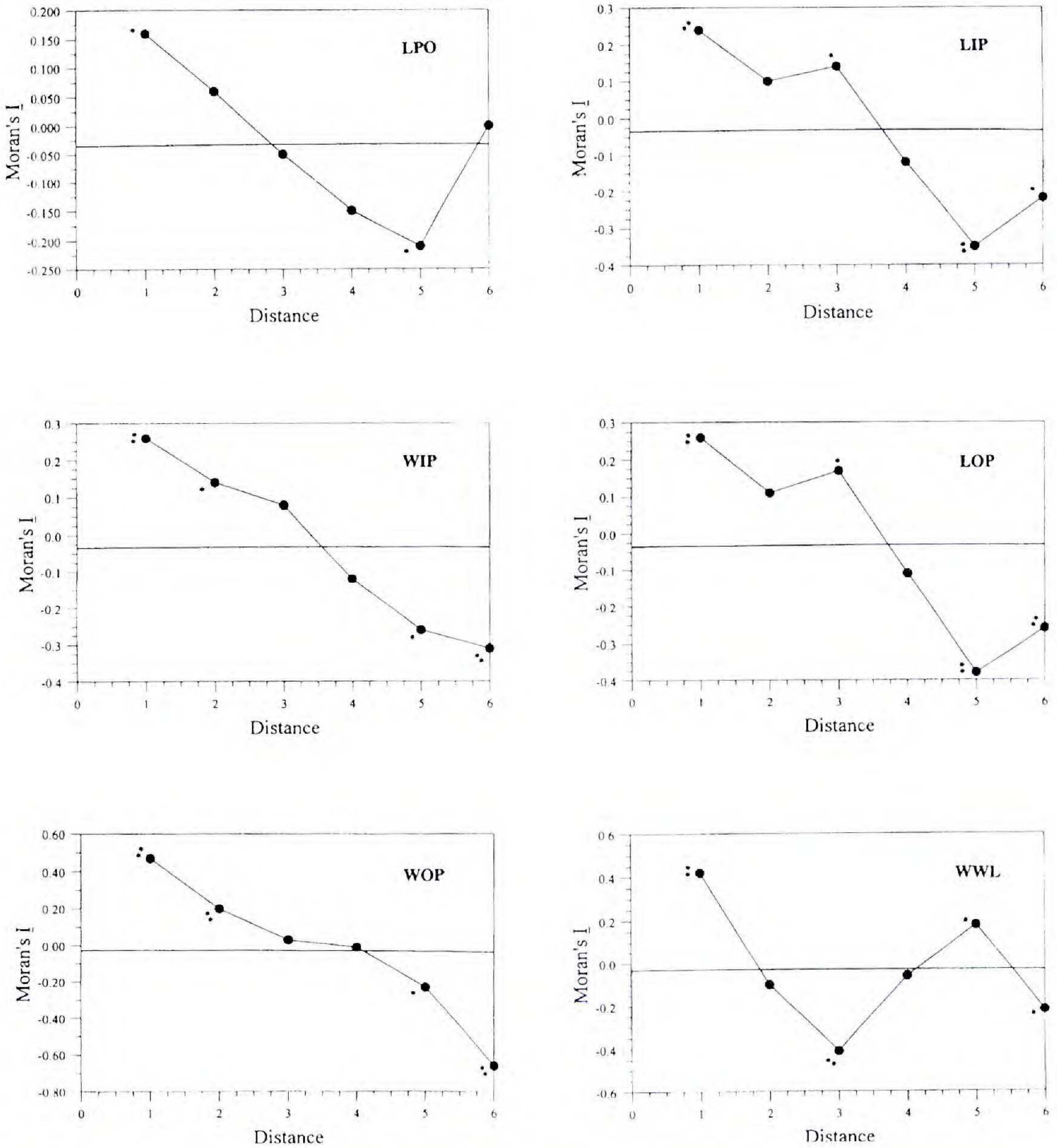

FIG. 3. Correlograms for LPO, LIP, WIP, LOP, WOP, and WWL. Significant autocorrelation coefficients ($P < 0.05$) are indicated by asterisks.

of the populations examined there are small patches whose diameter is less than interpopulational distances. The width of the lowest bracts and the longest leaves yielded a relatively long distance positive autocorrelation, which indicates these characters occur with circular or symmetrical gradients. It is of interest to note that the width of inner (WIP) and outer (WOP) perianth show a typical monotonic decline from significant positive autocorrelation at 67 to 102 Km to a significant negative autocorrelogram from 221 to 357 Km. Monotonicity is expected when separation by distance and gene flow between neighbor populations is the main factor.

The results of this study support the suggestions by Chung and Kang (1994) that there is a gradual transition of the floral morphology of *H. hakuunensis* from larger flowers in the central Korean Peninsula to smaller flowers in the southern Korean Peninsula. A similar pattern of geoclinal variation of floral morphology is previously reported in *H. dumortieri* complex in japan (Noguchi 1986), who noted that the flower tube enclosing the ovary and the length of the internal as well as external perianths exhibited a geoclinal variation. For example, northern populations possessed much shorter, somewhat thicker flower tubes and smaller perianths in comparison with those from southern populations.

In general, vegetative characters have much showed phenoplasticity than do reproductive characters in response to environmental and developmental factors (Stebbins 1950). It might be more reasonable to discuss the biological meanings of the results using reproductive characters. According to the criteria of Sokal and Oden (1978b), patterns such as those seen in several reproductive characters of *H. hakuunensis* might result from the combinations of gene flow via pollen and seed dispersal, founder effects, genetic drift, selective forces in patchy, isolated environments. More recently, we have analyzed the spatial distribution of genotypes using spatial autocorrelation of 28 alleles in populations (20 × 20–m) of *H. hakuunensis.* A genetic similarity was shared among individuals within 4.5 m distance, whereas an overall genetic dissimilarity among individuals beyond the distance, indicating that individuals in populations of *H. hakuunensis* occur on a gradient (Chung unpubl. data). Based on allozyme data obtained from 19 populations of *H. hakuunensis*, Kang and Chung (1997b) further suggested that gene movement and genetic drift may be primary factors for shaping population genetic structure among populations of *H. hakuunensis.*

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